Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

RELATION OF THE DAILY MARCH OF TRANSPIRATION TO VARIATIONS IN THE WATER CONTENT OF FOLIAGE LEAVES

Burton Edward Livingston and William Henry Brown[1]

Introduction

As was first pointed out in Publication 50 of the Carnegie Institution (1906), it is only by correcting the variations in the transpiration rate to uniform conditions of evaporation (that is, to a uniform evaporating power of the air), that anything approaching quantitative information concerning the seemingly almost autonomous changes in the rate of water loss from plants may be had. To accomplish this correction it is only necessary to consider the march of the ratio of the rate of transpiration to that of evaporation, the latter determined by means of some form of atmometer. This ratio has been termed *relative transpiration;* it denotes simply *the number of atmometers of the form used that would be necessary to evaporate the same amount of water as is lost by the transpiring plant in the same time and at the same place.* In other terms, relative transpiration is a measure of the equivalent or effective evaporating surface of the plant as this varies from time to time, the unit of evaporating surface being unit area of free water surface under properly defined conditions, or any other evaporating surface which may be adequately defined.

Reference to the nine graphs of relative transpiration presented in the publication just mentioned, and to the accompanying discussions, brings out the fact that the maximum of the evaporating power of the air (the evaporation rate from the porous cup atmometer in this instance) always occurred, in the cases cited, somewhat later in the day than did the maximum of relative transpiration (the ratio of transpiration rate to that of evaporation). This was interpreted to mean that some internal change had taken place in the leaves, which had begun to retard water loss even while the evaporating power of the air had still continued to increase. Such postulated change would not necessarily result in a decrease in the actual rate of water loss, thus forming a maximum point in the graph of *absolute* transpiration, but might merely *retard the increase* in this rate and thus give that graph a *lower slope* as it approaches its later-occurring maximum. The graph of *relative* transpiration, however, should show a definite maximum at the point when this retarding change was applied, since this graph is entirely independent of the direct effects of variations in the evaporating power of the air.

---

[1] Botanical contribution from the Johns Hopkins University, No. 22.

The maximum of absolute transpiration might occur at the same time as that of relative transpiration (when the postulated retarding influence may be considered as of greater magnitude than the accelerating influence of the still increasing evaporating power of the air), or it might occur later (when the acceleration due to the increasing evaporation rate may be considered as of greater influence than is the internal retardation). In fig. 8 of the publication to which we are referring, two of these maxima in the graph of absolute transpiration ("Rta") occur simultaneously with maxima in relative transpiration, while another occurs later than that in relative transpiration but earlier than the maximum in the graph of evaporation. The first two cases fulfil the former and the third the latter of the two suppositions made above.

In seeking to examine this daily retardation somewhat more closely, it was found (Publ. 50 still) that the maximum in relative transpiration thus evidenced might occur at almost any hour before the evaporation maximum, but that its occurrence usually fell in the hours between 10:00 A.M. and 1:00 P.M. This maximum, furthermore, appeared to be related to temperature. "As far as the limited data at hand can be trusted, the temperature of the surrounding air seems to be the controlling condition which governs this regulative response. . . . . There is some evidence that intensity of evaporation is the controlling factor, in some cases at least."[2]

From eleven cases on the graphs of the contribution just cited, we have calculated the amount of decrease in relative transpiration which was manifest at the time of the evaporation maximum. Thus, at its maximum, the relative transpiration ratio of *Euphorbia* (Publ. 50, Carnegie Inst., fig. 8) is 0.069, this ratio falling rapidly and becoming only 0.035 at the time when the highest evaporation rate for the day is reached. Thus, during the period indicated the retardation of relative transpiration has amounted to 50.8 per cent. On the second day this retardation amounts to 33.3 per cent. The average percentage decrease for the eleven cases is 48.6 per cent, there being little variation in the terms of the series (33.3 is the smallest, the next higher is 41.8, and the largest is 61.2), and we may conclude that the retardation in water loss, for this period, is about 49 per cent. It is improbable that there occurred any closing of stomata during the period involved in this calculation, for the maximum in the evaporating power of the air always occurred long before sunset. Indeed, the retardation which is manifest before any stomatal closing is to be expected is of a considerably higher magnitude than that taken in our calculation, so that the average value of this retardation is surely somewhat greater than that given here.

---

[2] LIVINGSTON, B. E., The relation of desert plants to soil moisture and to evaporation. Publication 50 of the Carnegie Institution, 1906, pp. 63–64.

With this approximation of the magnitude of the internal retardation of water loss, and with the above observation as to its time of occurrence in the day (10:00 to 1:00), we may attempt to ascertain what may be its probable cause.

Preliminary considerations

(1) INCIPIENT DRYING

In some recent studies[3] bearing upon the quantitative relation between the intensity of sunlight and transpiration, it has been emphasized more than heretofore how important an accelerating influence sunshine may exert upon the rate of water loss from green plants. This influence of solar intensity upon transpiration rate led the writer of the paper last cited to suggest that the internal retardation in water loss which occurs prior to the maximum rate of evaporation for the day may be due largely to an increase in the rate of *water loss itself*, as this may be brought about by a rise in the air temperature and especially by absorption of solar energy. This supposition has the appearance of a paradox, since the acceleration of a process is postulated as causing a retardation of the same process, but such phenomena are not infrequent where disturbances in the equilibrium of a system are dealt with, and the suggestion seems worthy of careful theoretical and experimental consideration.

---

[3] LIVINGSTON, B. E., (1) Light intensity and transpiration. BOT. GAZ. **52**:417–438. 1911.

———, (2) A radio-atmometer for comparing light intensities. Plant World **4**: 96–99. 1911.

On purely a-priori grounds it is readily understood from the principles of thermodynamics, that a rise in the temperature of the air which bathes the leaves (such as normally progresses throughout the forenoon and well into the afternoon) should produce an ever-increasing vapor pressure of water within the internal atmosphere of the foliar tissues and over the cuticular surfaces. Such an increase in vapor pressure within would usually be adjusted *pari passu* with the rise in temperature, by the ejection of an increasing amount of water vapor through the stomatal openings, and if the temperature were to remain constant for a time the rate of water loss during such a period would be somewhat greater than at the lower temperature, the slightly greater rate being due to the more rapid vaporization and diffusion at higher temperatures.

But the rise in temperature of air and of leaf are not our main consideration with reference to openly exposed green foliage upon a sunny day. Air and leaf do continuously increase in temperature from early morning till some time in the afternoon, but in the meantime the radiant energy of the sunshine is ever being absorbed to a greater or less extent by the green leaf tissue, so that this tissue should tend to become warmer than the air. By far the larger portion of this absorbed energy (a negligible portion disappears through photosynthetic changes) must operate to increase the vapor tension of the water films which surround the foliar air spaces or are held in the epidermal walls. Evaporation from these films must thus be increased, the latter remaining nearly constant in temperature. The accelerated evaporation within the leaf should produce in its turn an increase in the partial gas pressure due to water vapor in the internal atmosphere, and hence, the stomata being open, a more rapid diffusion, or possibly a molar movement,[4] of water vapor through these openings into the outer air. As long as the sun shines, then, a high rate of transpiration may be maintained, and this without excessively high temperatures in the foliar tissues. The radio-atmometer (LIVINGSTON, see footnote 3) furnishes an excellent example of this kind of effect; with continuous influx of solar energy evaporation from the black porous cup is maintained at a high rate, but the black cup does not exhibit any markedly higher temperature than does the white one, from which water loss is much less rapid.

The Piche atmometer[5] illustrates this process, and also shows another phenomenon which we need to consider here. It consists of a graduated glass tube, closed above and covered below with a circle of filter paper, the latter having a pin hole to admit air to the tube. The tube is filled with water, the paper disk applied and fixed in place, and the whole inverted. The entire disk soon becomes wet, and evaporation therefrom draws water from the tube, air rising through the pin hole to replace the water withdrawn. Now, if such an instrument be arranged with a relatively large disk of paper and placed in conditions of pronounced evaporation, it may often be noted (we are unable to find any mention of this in the literature) that the outer edge of the disk becomes dry, thus vitiating the readings as a measure of the evaporating power of the air. The instrument is unsuited to its purpose unless care be exercised to have the paper so small that the evaporation rate never surpasses the possible rate of outward diffusion to the periphery of the disk. As long as the peripheral portion of the paper remains unsaturated, the actual rate of water loss is maintained nearly constant, the dry area automatically increasing or decreasing in extent according to the fluctuations in the amount of energy

[4] According to the researches and calculations of BROWN and ESCOMBE (Static diffusion of gases, etc., in plants. Phil. Trans. Roy. Soc. London **193**:223–291. 1900), no molar or streaming movement needs to be postulated to explain the highest rates of transpiration observed by these authors in southern Britain. Whether a molar streaming may not occur about midday in the Arizona desert remains an open question.

[5] For literature bearing on this instrument, see LIVINGSTON, GRACE J., An annotated bibliography of evaporation, reprinted from Monthly Weather Review, 1908–1909. The original description is abstracted at page 48 of the reprint under "1872, Piche."

absorbed. Thus, an increase in the evaporating power of the air or in the intensity of impinging solar energy may, with such an instrument, bring about an actual decrease in the extent of the evaporating surface and hence a retardation of water loss. While the actual rate of water loss remains constant so long as the paper is not completely wet, the *relative* rate of water loss (as the loss from the instrument might be compared with that from an open pan of water similarly exposed) begins to decrease as soon as the peripheral portion of the paper begins to dry out. Of course the drying of the disk and the accompanying retardation of relative evaporation are due to a fall below unity of the ratio of possible water supply to water loss; since the rate of possible supply in this instrument remains constant, this means an increase in the denominator of the ratio. A similar result might be occasioned if the rate of loss were to remain constant and the rate of possible supply were to be decreased.

This sort of inadequacy in the rate of water supply to maintain the original evaporating surface during periods of high evaporation may be postulated as perhaps the main feature in bringing about the somewhat sudden fall in relative transpiration observed in the early portion of the day. Indeed, a Piche atmometer may be so arranged, with an abnormally large, preferably *blackened*, disk, so that if compared to a pan of water or to a porous cup atmometer it will exhibit a graph of *relative evaporation* for the daylight hours quite closely paralleling the corresponding graph of relative transpiration for a green plant similarly exposed.

It is only logically conceivable that there exists, for each leaf at any particular time, a maximum possible rate of inward movement of water through the petiole, and if the rate of water loss at any time surpass this possible rate of supply, the tissues of the leaf should become less moist, following the analogy of the Piche atmometer described above. This supposed process of drying out of the foliar cell walls which abut upon the internal atmosphere has been termed *incipient wilting*[6] by the author last cited. It should take place rapidly at first and more slowly later, the water films gradually retreating into the pores of the cellulose and not only decreasing the extent of the exposed evaporating surfaces, but also greatly increasing the surface tension of the latter. When the surface tension of a liquid film is increased, its vapor tension is correspondingly decreased,[7] so that incipient drying of these exposed cell walls should be accompanied by a marked fall in the rate of vaporization of water therefrom. This should mean nothing less than a measurable retardation in the relative rate of water loss, a retardation *due to an excessive evaporation rate.*[8]

---

[6] Since an *incipient* process must be regarded as already actually occurring, it is quite illogical to apply the term *wilting* to a condition of affairs which by definition is not accompanied by any wilting at all. We have therefore adopted the term *incipient drying* in place of the other term.

A physical parallel of this phenomenon may readily be arranged by mounting one of two similar paper disks as in the Piche atmometer, so that it will be constantly supplied with water, and its water content will remain constant during the progress of evaporation, while the second disk is similarly mounted on an empty tube, so that its moisture content will fall with water loss. An experiment of this sort, carried out by weighings in the laboratory, showed that a fall in the moisture content of the paper of 6 per cent produced a corresponding decrease in the rate of evaporation of 5 per cent. Similarly, a fall of 17 per cent in water content was accompanied by an evaporation rate 8 per cent lower than when the paper was saturated. The effect becomes more and more pronounced as the paper dries out; when only 54 per cent of the original moisture was present the rate of water loss had diminished to 77 per cent of that from the saturated disk.

---

[7] PATTEN, H. E., On the relation of surface action to electrochemistry. Trans. Am. Electrochem. Soc. **19**:359–380. 1911. Also, FREUNDLICH, H., Kapillarchemie. Leipzig. 1909. p. 46.

DIXON has presented the only experimental evidence of this with which we are acquainted. DIXON, H. H., Transpiration and the ascent of sap. Prog. Rei. Bot. **3**:1–66. 1909. p. 51.

[8] RENNER has pointed out this same thing: "Denn wenn die Wasserzufuhr ausbleibt, müssen die Membranen trockener werden und damit die Transpiration weiter sinken. . . . ." RENNER, O., Beiträge zur Physik der Transpiration. Flora **100**: 451–547. 1910. p. 516; see also p. 520.

The same author has contributed a most excellent analysis of the water relations of stem and leaf, many points of which have a bearing upon the present question, but we are unable to do more here than merely to mention the paper: RENNER, O., Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**:171–247. 1911.

If the cellulose membranes which are adjacent to the air spaces of the leaf and those bathed by the outer air were structurally similar to the filter paper used in the test just described, the above figures might be applied to the moist foliar surfaces. But we may be sure that filter paper possesses a much less compact structure than any cell membrane in the plant; hence, the reduction in the evaporation rate brought about by partial drying out of the moist cell walls should be much more marked in the case of the latter than is manifest in our experiment. It seems quite probable that a reduction of 50 per cent in the water content of exposed cellulose walls should produce an equal or much greater reduction in the evaporation rate therefrom, and in the case of cutinized epidermis (which holds but little moisture when saturated, and from which cuticular transpiration takes place), the effect of partial drying out should be still greater.

It appears, therefore, quite within the limits of possibility, that the phenomenon of incipient drying of exposed membranes (internal and external) may be adequate to cause the non-stomatal hindrance to transpiration here considered. It should make no difference whether the excessive rate of water loss from foliage leaves be brought about by high evaporating power of the air, by absorption of sunshine, by continually rising temperature, or (merely relatively) by a decrease in the possible rate of water supply (as by the drying of the soil or by the removal or injury of the basal part of the plant), the effect must be the same in every case, namely, a marked fall in the rate of relative transpiration.

If such a process of drying out in leaf tissue were continued, water would eventually be extracted from the protoplasmic membranes, which would in turn remove moisture from the vacuoles, and (since we suppose that the rate of supply from the vascular elements to be inadequate) the turgor pressure would decrease. Finally, all internal pressure would be removed from the cell walls, which would thus cease to be under strain, and all turgidity would thus be destroyed; the wilting point would be reached. Continued still further, the process would result in actual plasmolysis of the cells and finally in death, after which desiccation would rapidly take place. The latter portion of this supposition seems applicable in all cases when leaves wilt and dry through the influence of too great an intensity of transpiration or too low a maximum possible rate of water supply, these two causes being merely different aspects of the same condition, namely, that the ratio of supply to demand is less than unity.

(2) OTHER POSSIBLE FACTORS IN THE PRODUCTION OF AN INTERNAL RESISTANCE TO WATER LOSS

Logically, there are other possible causes for the observed fall in relative transpiration; it might be regarded as brought about by increased concentration either of the extracellular liquid (in and upon the cell walls), or of the cell sap within the cell vacuoles (as by photosynthesis), or by decreased permeability (perhaps some sort of hardening or coagulation) of the protoplasmic layer itself. The recent work of FITTING[9] shows that the osmotic pressures in the vacuoles of the foliage of desert plants in moist soil (these conditions agree with those of LIVINGSTON'S plants) are usually isosmotic with a solution less concentrated than 2-molecular potassium nitrate. The fact that no wilting was apparent in the Arizona experiments upon which we are basing our work (which means that turgidity was maintained) indicates clearly that the concentration of the cell sap must have been *higher* than that of the extracellular solutions. Thus the maximum concentration of the evaporating solutions which can be postulated is surely no greater than that of a 2-molecular solution of potassium nitrate, and in order to be certain that our error is in the right direction, we may assume maximum concentrations isosmotic with a 3-molecular solution of this salt. The minimum concentration (as in the early morning) can never be zero, but we once more take this as an assumed limit far beyond the actual, and ask the question, if the foliar solutions vary from pure water to a concentration isosmotic with 3-molecular potassium nitrate, what may be the relative magnitude of the resulting retardation of evaporation? Other conditions being equal, evaporation is known to be proportional to the vapor tension of the evaporating surface, and the vapor tension (and hence the evaporation) of a 3-molecular solution of potassium nitrate is only about 8 per cent lower than that of pure water. A comparison of this figure with 49 per cent, the approximated retardation in transpiration, leads us to conclude that an increased concentration and the accompanying lowerings of vapor tension of the foliar solutions cannot possibly be directly related to the great fall in relative transpiration which is observed.[10] That such variations in concentration may have some indirect effect is highly improbable, and there is no evidence at hand to enable us to consider this possibility here. That a slight diurnal increase in the concentration of solutions bathing the protoplasmic membranes might bring about marked changes in the colloidal state of the latter, and hence in their permeability to water, is of course possible; but if such were the case, the effect would be manifest simply as a lowering of the possible rate of supply to the cell walls, resulting in a partial drying out of these, so that the phenomenon would appear as incipient drying.

---

[9] FITTING, HANS, Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeitschr. Bot. **3**:209–275. 1911. See also LIVINGSTON, B. E., The relation of the osmotic pressure of the cell sap in plants to arid habitats. Plant World **14**:153–164. 1911.

We conclude, therefore, that the hypothesis of incipient drying, due to partial drying of exposed membranes, is the only adequately possible explanation of the diurnal fall in relative transpiration. If this process actually occurs, it should be exhibited in a sensible decrease in the actual moisture content of the leaves concerned. We should thus expect to find the moisture content of sun-illuminated foliage to become less as the day advances, attaining a minimum some time in the afternoon and then rising again. Whether or not this is actually manifest, as a diurnal fall in the percentage of foliar moisture, is the question which we have experimentally attacked.

It needs to be added here that the hypothesis of incipient drying, while apparently the only logically possible explanation of the non-stomatal *hindrance to water loss*, is not the only logically possible cause of a marked diurnal *fall in the relative water content of* green leaves. With the actual water content of the tissues remaining constant, a diurnal accumulation of non-aqueous materials, as of carbohydrates, oils, proteins, etc., might result in a great increase in the contained non-aqueous material, and a corresponding fall in the percentage of moisture. Such an accumulation, with its accompanying decrease in the percentage of moisture, however, would have no marked influence upon relative transpiration. This question may be studied quantitatively through the daily fluctuations in relative water content on the basis of unit leaf area, a phase of the problem with which we have not concerned ourselves.

---

[10] This conclusion is quite in accord with that reached by DRABBLE and DRABBLE. See DRABBLE, E., and DRABBLE, H., The relation between the osmotic strength of cell sap in plants and their physical environment. Biochem. Jour. **2**: 117–132. 1907.

Experimentation

Our method of experimentally attacking the problem as to whether a definite diurnal fall in the percentage of leaf moisture actually occurs was to gather, at different hours of the day and night, a large number of similar leaves from plants growing in the open soil, and to determine the percentage of moisture therein contained by the common method of weighing, drying at 100° to 105° C., and reweighing. As the leaves were gathered they were placed immediately in tarred glass bottles and tightly stoppered. After being weighed, the open bottles were placed in the drying oven, and the final dry weight obtained without removing or handling the leaves. A large number of plants were available for this work, so that but few leaves were taken from the same plant, and the numerical result may be taken as fairly well approximating the average condition of the whole plot of plants of the species tested. The plants used were all spontaneous in the open ground near the Desert Laboratory. In some cases the sample leaves were taken every two hours, in others less often, and a porous cup atmometer was operated and read at short intervals in the vicinity of the group of plants from which leaves were taken. The work was carried out at the Desert Laboratory of the Carnegie Institution at Tucson, Arizona, in the summer of 1910.

Preliminary tests of the leaf moisture in *Physalis angulata* var. *Linkiana* Gray and in *Martynia louisiana* Mill., made on July 28, showed that the moisture content of the *Physalis* leaves was 744.7 per cent of the dry weight at 6 A.M., and only 561.0 per cent at 2 P.M., while the corresponding percentages in *Martynia* leaves were

543.3 and 377.3 per cent, respectively. Expressed in another way, the non-aqueous materials of the leaves made up for *Physalis* 12 per cent of the whole in the morning and 15 per cent in the afternoon, while for *Martynia* these quantities were 16 and 21 per cent, respectively. It thus became clear that there had occurred a marked fall in the relative moisture content of these leaves during the period from 6 A.M. to 2 P.M., which is what our a-priori considerations had led us to expect, and our problem seemed to be answered in the affirmative.

We present, in the four following tables, the data derived from a number of other tests, carried out by a method quite similar to that followed in the two tests just described. Besides the two plants named above, we dealt with *Nicotiana glauca* Graham (a woody perennial attaining the proportions of a tree), *Euphorbia heterophylla* L., *Trianthema Portulacastrum* L. (a fleshy plant resembling *Portulaca oleracea* L. of the east), *Tribulus terrestris* L., *Sida angustifolia* Lam., *Amarantus Palmeri* Wats., *Maclura pomifera* (Raf.) Schneider, *Covillea glutinosa*, and *Prosopis velutina* Wooton. The two last-named plants are characterized by thin, hard, xerophyllous leaves, the foliage of *Covillea* (the creosote bush) being heavily covered with a shellac-like resinous layer. For the naming of our experimental plants we are indebted to the kindness of Professor J. J. THORNBER, of the University of Arizona.

Tables I to IV present the evaporation rates for the periods in question, in terms of cc. from the standard porous cup atmometer.[11] The moisture contents of the leaves are given in percentages of their dry weight, also the dry weights in percentages of total weight. In the first two columns appear periods and evaporation rates per hour (cc.) from the porous cup atmometer, these data being quite comparable throughout all four series. Evaporation maxima are designated by asterisks. In the third column are presented the hour at which leaf tests were made. The remainder of each table presents the leaf moisture data, each minimum being denoted by an asterisk in the second column for each plant, and all the maxima by full-faced type.

---

[11] LIVINGSTON, B. E., Operation of the porous cup atmometer. Plant World **13**:111–118. 1910.

It is at once apparent that in all cases but three (nine out of eleven species) our question (page 319) has been answered very definitely in the affirmative.[12] In the case of *Prosopis* (table III) the minimum water content, at midday, is only slightly below that in the early morning, and the maximum, at 4 P.M., is not markedly above the minimum; this case is questionable. One of the two definite exceptions to the general rule, *Covillea* (table III), appears to exhibit a reversal of the usual variation in water content. The fact that this plant and *Prosopis* are non-succulent xerophytes is

TABLE I

AUGUST 12–13, 1910

EVAPORATION		PERCENTAGE OF MOISTURE						
			Martynia		Sida		Amarantus	
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)								
6– 7	0.66	6	417.6	81	452.8	82	539.4	84
7– 8	1.14	7	390.0	80	**484.3**	**83**	533.3	84
8– 9	2.28	8	394.6	80	412.5	80	551.2	85
9–10	2.34	10	384.2	79	353.7	78	500.7	83
10–11	2.58	. .	. . . . .	. .	. . . . .	. .	. . . . .	. .
11–12	2.52	12	357.6	78	355.7	78	490.6	83
(P.M.)								
12– 1	3.48	. .	. . . . .	. .	. . . . .	. .	. . . . .	. .
1– 2	3.90	2	339.3	77	338.9	77	395.0	80
2– 3	3.54	. .	. . . . .	. .	. . . . .	. .	. . . . .	. .
3– 4	3.72	4	338.4	77*	307.3	75*	379.6	79
4– 5	4.02*	. .	. . . . .	. .	. . . . .	. .	. . . . .	. .
5– 6	2.52	6	371.2	79	317.1	76	366.6	79*
6– 7	1.56	. .	. . . . .	. .	. . . . .	. .	. . . . .	. .
7– 8	1.44	8	**551.6**	**85**	407.2	80	591.5	86
8– 9	1.32	. .	. . . . .	. .	. . . . .	. .	. . . . .	. .
9–10	1.08	10	502.7	83	444.4	82	539.2	84
10–12	0.69	12	461.5	82	457.1	82	**601.9**	**86**
(A.M.)								
12– 4	0.125	4	494.7	83	457.0	82	530.0	84
4– 5	0.72	. .	. . . . .	. .	. . . . .	. .	. . . . .	. .
5– 6	0.60	6	455.1	82	. . . . .	. .	542.1	84

---

[12] At about the same time that our experiments were in progress, LLOYD carried out his recently published tests in regard to this same matter in *Fouquieria*. He finds and discusses a diurnal fall in the relative water content of the foliage of this plant. LLOYD, F. E., The relation of transpiration and stomatal movements to the water content of the leaves in *Fouquieria splendens*. Plant World **15**:1–14. 1912.

possibly to be correlated with their peculiar behavior, and it may be suggested that such permanent structural retardation of water loss as is present in the foliage of such types may have to do with preventing a marked decline in leaf moisture by day. Such plants seem worthy of further study in this connection. The other exception to the usual behavior is that of *Physalis* (table IV). For this species we have two cases exhibiting the usual behavior (besides the preliminary test, which makes three), and it is noted that the exceptional case occurs on a day with very low evaporation.

TABLE II

AUGUST 21–22, 1910

EVAPORATION		PERCENTAGE OF MOISTURE										
			Physalis		Nicotiana		Euphorbia		Trianthema		Tribulus	
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)												
4– 5	0.06	5	......	..	**588.7**	**85**	......	..	......	..	**435.6**	**81**
5– 6	0.06	..	......	..	......	..	......	..	......	..	......	..
6– 7	0.50	7	820.2	89	......	..	**581.6**	**85**	**1203.9**	**92**	......	..
7– 8	1.20	..	......	..	......	..	......	..	......	..	......	..
8– 9	1.92	9	865.5	90	435.0	81	521.6	84	1197.9	92	352.5	78*
9–10	2.10	10	804.6	89	......	..	......	..	......	..	......	..
10–11	2.40	11	818.9	88	......	..	......	..	......	..	......	..
11–12	2.58	..	......	..	......	..	......	..	......	..	......	..
(P.M.)												
12– 1	2.40	1	678.5	87	423.3	81	433.8	81*	758.0	89*	378.8	79
1– 2	2.88	..	......	..	......	..	......	..	......	..	......	..
2– 3	2.94*	3	660.6	87*	......	..	......	..	......	..	......	..
3– 4	2.70	..	......	..	......	..	......	..	......	..	......	..
4– 5	2.70	5	703.4	87	392.5	80*	485.5	83	825.2	89	420.1	81
5– 6	1.92	..	......	..	......	..	......	..	......	..	......	..
6– 7	1.20	7	**877.9**	**90**	......	..	......	..	......	..	......	..
7– 8	1.20	..	......	..	......	..	......	..	......	..	......	..
8– 9	1.20	9	855.7	90	......	..	480.9	83	......	..	430.6	81
9–10	0.90	..	......	..	......	..	......	..	......	..	......	..
10–11	1.98	..	......	..	......	..	......	..	......	..	......	..
11–12	1.14	..	......	..	......	..	......	..	......	..	......	..
(A.M.)												
12– 1	0.42	..	......	..	......	..	......	..	......	..	......	..
1– 2	0.42	..	......	..	......	..	......	..	......	..	......	..
2– 3	0.18	3	848.2	89	......	..	......	..	......	..	......	..

Table V presents a summary of the data of the preceding tables. The minimum and maximum water content and the hours at which these occurred, the latter being simply numbered from 1 to 24, are there given, together with the corresponding maximum rate of evaporation and the hour of its occurrence.

TABLE III

August 28–29, 1910

Evaporation		Percentage of moisture								
			Physalis		Maclura		Covillea		Prosopis	
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)										
6– 7	0.82	7	778.5	89	**237.2**	**70**	116.7	54*	159.7	61
7– 8	2.37	..	.....	..	.....	..	.....	..	.....	..
8– 9	2.87	9	736.7	88	224.1	69	127.4	56	145.3	59
9–10	3.77	..	.....	..	.....	..	.....	..	.....	..
10–11	4.51	11	595.2	86	.....	..	.....	..	.....	..
11–12	4.92	..	.....	..	.....	..	.....	..	.....	..
(P.M.)										
12– 1	5.08*	1	566.2	85*	186.6	65	125.1	56	144.3	59*
1– 2	4.67	..	.....	..	.....	..	.....	..	.....	..
2– 3	3.03	3	625.9	86	173.8	63*	.....	..	.....	..
3– 4	3.69	4	.....	..	.....	..	**139.3**	**58**	**168.4**	**61**
4– 5	2.13	5	780.6	89	.....	..	.....	..	.....	..
5– 6	1.56	..	.....	..	.....	..	.....	..	.....	..
6– 7	1.15	7	**781.1**	**89**	.....	..	.....	..	.....	..
7– 8	1.56	..	.....	..	.....	..	.....	..	.....	..
8– 9	0.90	9	772.1	89	186.9	65	.....	..	.....	..
9–10	0.90	..	.....	..	.....	..	.....	..	.....	..
10–11	0.57	11	761.5	88	.....	..	.....	..	.....	..
11–12	0.49	..	.....	..	.....	..	.....	..	.....	..
(A.M.)										
12– 1	0.74	1	696.1	87	.....	..	.....	..	.....	..
1– 2	0.33	..	.....	..	.....	..	.....	..	.....	..
2– 3	0.41	3	705.4	88	.....	..	.....	..	.....	..
3– 4	0.33	..	.....	..	.....	..	.....	..	.....	..
4– 5	0.33	5	743.4	88	.....	..	.....	..	.....	..
5– 6	0.82	..	.....	..	.....	..	.....	..	.....	..
6– 7	1.48	7	755.2	88	.....	..	.....	..	.....	..

Physalis is the only form which was tested on different days, with different conditions of evaporation, and the data therefrom are the most instructive of our series. In the first two cases this form showed the greater variation in water content with the higher evaporation maximum (5.08 cc. per hour, table III), and the smaller variation with the lower evaporation maximum

(2.94 cc. per hour, table II). In the third test the water variation was slightly (probably within the limits of experimental error) in the opposite direction, as has been noted. The evaporation maximum on this day was relatively low, 2.52 cc per hour (table IV). These relations make it appear that the amount of variation in foliar moisture is directly related to the evaporating power of the air, especially to the maximum intensity of this factor for the day in question. With great evaporation there appears to be a great diurnal fall in moisture content, with less evaporation a less pronounced fall, and with still less evaporation no fall at all, possibly even a slight rise.

TABLE IV

AUGUST 30, 1910

EVAPORATION		PERCENTAGE OF MOISTURE		
			Physalis angulata	
Period	cc. per hour	Hour of test	On basis of dry substance	On basis of entire weight
(A.M.)				
7– 8	1.97	7	668.2	87
8– 9	1.56	9	695.0	87
9–10	1.72	..	.....	..
10–11	2.46	11	680.7	87
11–12	2.30	..	.....	..
(P.M.)				
12– 1	2.30	1	**714.7**	**88**
1– 2	2.52*	..	.....	..
2– 3	2.30	3	662.3	87*
3– 4	2.30	..	.....	..
....	....	..	.....	..
4:30–5:30	0.97	5:30	665.7	87

NOTE.—The day was almost wholly cloudy, which accounts for the generally low evaporation rates and the small fluctuations.

Only a single test, with measurement of evaporation, was carried out with each of the remaining forms. The greatest variations were exhibited by *Martynia*, *Amarantus*, and *Sida*, all of them being plants which have been repeatedly observed to wilt very readily under drought conditions. The only true succulent tested was *Trianthema*, which showed a variation markedly greater than that of *Physalis* for the same day (table II). *Nicotiana* and

Euphorbia gave variations equaling *Physalis* (tables II and III); those of *Tribulus* and *Maclura* were markedly less; while, as already noted, *Prosopis* and *Covillea* evidence very small variations, that of the latter rather definitely in the opposite direction.

Scrutiny of table V brings out the fact that the hours of minimum relative water content for the prevailing type of leaves falls generally within an hour or two of that of the maximum evaporation rate. The minimum moisture content occurs between 1:00 P.M. and 5:00 P.M. for all cases except those already noted as exceptional, and that of *Tribulus* (table II), which has its minimum at 9:00 A.M.

TABLE V

SUMMARY OF TABLES I–IV

PLANT	MINIMUM MOISTURE CONTENT		MAXIMUM MOISTURE CONTENT		MAXIMUM OF EVAPORATION	
	Percentage	Hour	Percentage	Hour	cc.	Hour
Martynia (table I)..	77	14	85	20	4.02	16–17
Sida (table I)......	75	16	83	7	4.02	16–17
Amarantus (table I)	79	16, 18	86	20, 24	4.02	16–17
Physalis (1) (table II)	87	13, 16	90	19, 21	2.94	14–15
Physalis (2) (table III)......	85	13	89	17, 19, 21	5.08	12–13
Physalis (3) (table IV).......	87	15, 17½	88	13	2.52	13–14
Nicotiana (table II)	80	17	85	5	2.94	14–15
Euphorbia (table II)	81	13	85	7	2.94	14–15
Trianthema (table II).......	89	13, 17	92	7, 9	2.94	14–15
Tribulus (table II)..	78	9	81	5, 17, 21	2.94	14–15
Maclura (table III).	63	15	70	7	5.08	12–13
Covillea (table III).	54	7	58	16	5.08	12–13
Prosopis (table III).	59	9, 13	61	7, 16	5.08	12–13

The evidence from *Physalis*, indicating clearly a definite relation between the magnitude of the moisture variation and the intensity of evaporation, may be interpreted to mean that the variation is due primarily to incipient drying (to a removal of water by transpiration more rapidly than its entrance into the leaves), and not to an accumulation of non-aqueous bodies in the leaf cells. It seems extremely improbable that a diurnal accumulation of plastic materials should exhibit such a parallelism with the evaporation as do our data of moisture variation, from which consideration it may be concluded that the variation is probably not causally related to such accumulation of substances. While there are several observations in the literature which bear more or less directly upon this matter of the diurnal accumulation of soluble and insoluble bodies in the leaf, we do not as yet possess data adequate to a logical discussion. This should be made the subject of a special study in the present connection.

Following the criterion of the *time of occurrence* of the minimum water content (2 to 5 P.M.) and of that of the maximum in relative transpiration, as brought out in Publ. 50, Carnegie Inst. (10 A.M. to 1 P.M.), it appears highly probable that there exists a causal relation between these two phenomena. Since the critical point in the graph of relative transpiration denotes, as has been pointed out, the entrance into operation of some internal check or hindrance to the loss of water vapor, and since a decrease in relative water content should be effective to produce such a check long before the water content had attained its minimum, we should expect the maximum in relative transpiration to occur long before the hour of least foliar moisture, which it appears actually to do. We may conclude tentatively, and on general lines, that, for the ordinary types of leaves, the retardation in water loss is manifest several hours before the time of minimum water content. After the critical point in relative transpiration, the non-stomatal retardation of water loss appears to be (Publ. 50) continuously active until well into the night, its effects becoming mingled with those of stomatal closure at or about sunset. It appears to be gradually removed during evening and early night, so that in the hours just preceding sunrise stomatal retardation seems to be alone manifest. If the non-stomatal effect be due to decreased water content, it should be removed when the leaves had regained their normal moisture, which condition is quite met by the observations. The maximum in moisture content (except in the few erratic cases already mentioned) occurs in the night or early morning, just as our hypothesis demands.

The only direct comparison between the daily march of leaf moisture and that of relative transpiration which has been made thus far, was carried out on August 21 and 22. From 5 A.M. on the first day till 6 A.M. on the second, hourly weighings were made on two potted and sealed plants of *Physalis*, while corresponding readings were obtained from a porous cup atmometer having the same exposure. The two plants were similar to each other and, though somewhat smaller, not dissimilar to the *Physalis* plants of the leaf moisture tests of the same period (table II), so that the two series of data are fairly comparable. Space will not permit the presentation here of the transpiration and evaporation rates and of the resulting ratios and graphs, but we may mention the findings of most present interest. Averaging the data for the two plants (these data are very similar), the maximum of absolute transpiration occurred from 11 A.M. to 12 noon, while the maximum rate of loss from the porous cup atmometer fell three hours later. The maximum of relative transpiration occurred from 12 noon to 1 P.M.; thus the non-stomatal retardation of water loss became effective about 1 P.M. As already shown (table II), the moisture content of the leaves of *Physalis* in the open soil fell during the period from 9 A.M to 3 P.M., and rose again to its maximum, or what we may term its normal, at 7 P.M. From these data we see that the non-stomatal retardation of water loss became manifest in the potted plants four hours after the leaf moisture had begun to decrease in the plants in the open, and two hours before the occurrence of the minimum water content. The maximum evaporation rate occurred in the hour preceding the minimum water content. All of these points are quite in harmony with the requirements of the hypothesis of incipient drying, and the data appear to substantiate this hypothesis, so far as their incomplete nature will allow.

The work of BRIGGS and SHANTZ[13] on some of the conditions which determine wilting has thrown not a little indirect light upon the question of the occurrence of incipient drying. By the ingenious balanced system which these authors devised, they have shown clearly that, with the gradual drying out of the soil, there comes a time when the rate of entrance of water into the upper part of a plant is surpassed by the transpiration rate. This is, of course, the condition of incipient drying. Judging from the rates of transpiration shown by the tables of this contribution (no attempt is made to define the aerial conditions), it appears that the evaporating power of the air during the experiments there described was relatively low. This fact rendered the process of incipient drying, which leads eventually to actual wilting, very much prolonged, and it is perhaps not surprising that these authors failed to detect incipient drying in the plants which actually wilted, making the mistake of supposing that incipient drying in the non-wilting forms (as cactus, lemon, etc.) is to be considered as identical with actual wilting (which is relatively a much later occurrence) of ordinary thin-leaved plants. It is greatly to be regretted that such an expensive and elaborate series of determinations as BRIGGS and SHANTZ have made should have been carried out without records of the intensity and duration aspects of the evaporating power of the air under which the experiments were performed. Such records, which are perhaps the most readily obtained of all the climatic records which are as yet available for the study of plant processes, would have made possible the duplication of the aerial conditions of these experiments and would have aided greatly in the further analysis of some of the important findings of these authors.

---

[13] BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient for different plants and its indirect determination. Bur. Pl. Ind. Bull. 230. 1912.

Conclusions

We conclude from our measurements and comparisons that there can remain little question that green plants when subjected to relatively great diurnal evaporation intensity, at least frequently exhibit a marked fall in foliar moisture content by day and a corresponding rise by night. The daily march of evaporation remains still to be studied in other climates than that of summer in southern Arizona, so that we are unable to compare our conditions with those of more humid or cooler regions. From our experience with cloudy weather, we are inclined to the prediction that the diurnal decrease in leaf moisture here established for high evaporation rates may fail to occur in regions of low evaporation when accompanied by relatively high rates of soil moisture supply.

Our studies also indicate that some non-succulent, small-leaved xerophytes (such as *Covillea* and *Prosopis*) fail more or less completely to exhibit a diurnal fall in foliar moisture under conditions of evaporation which render it manifest in the common type of thin-leaved plants (such as *Martynia*, *Sida*, *Physalis*), as well as in such pronounced succulents as the *Portulaca*-like *Trianthemum* of our work. It is suggested that these exceptional small-leaved xerophytes may actually show a somewhat higher leaf moisture content by day than by night, but this proposition is uncertain.

While the other logically possible cause of this diurnal decrease in relative water content of foliage leaves, namely, a diurnal increase in materials other than water within the tissues, remains still to be considered in a thoroughly adequate way, our findings fail to adduce evidence in favor of this as the true cause of the observed phenomena, and do furnish several lines of indirect opposing evidence. It may be stated, therefore, that, so far as evidence is at hand (including indirect considerations of the literature, not here cited), it is probable that the cause of this diurnal minimum in foliar moisture rests in the phenomenon of incipient drying, brought about whenever the ratio of water loss to water supply in the leaves is rendered less than unity. It may thus be suggested that, although our tests with *Physalis* would lead to the conclusion that the external factor which controls this diurnal fall of leaf moisture is evaporation intensity simply, the true controlling condition is more probably the ratio of water supply to water loss. Thus, the structure of the plant (including all of its various "adaptations" to dry habitats), the moisture conditions of the soil, intensity of evaporation and of solar illumination appear to make up the controlling environmental complex.

It seems highly probable from our studies that the diurnal, non-stomatal retardation of the escape of water vapor from green leaves in sunlight (as first described in Publ. 50, Carnegie Inst., and there attributed to the influence of temperature or evaporation intensity) is but the effect of a lower vapor tension within the internal atmosphere of the leaves and over their surfaces, this lower vapor tension being brought about by the increased surface tension and decreased evaporating surface which accompanies a lowered water content of the internally and externally exposed cell walls.

In conclusion, it may be suggested that we have here, in the diurnal minimum in the water content of foliage leaves, a criterion that may be of some importance to scientific agriculture, at least in the arid regions of the globe. By this criterion it may be possible to determine indirectly, and somewhat simply, the status of the water relations of the plant, and indeed to foresee the need of increased soil moisture, long before the usual criterion of cessation of growth or actual wilting becomes manifest.

THE JOHNS HOPKINS UNIVERSITY
BALTIMORE, MD.

BUREAU OF SCIENCE
MANILA, P.I.